U-SHAPED ORIENTATION OF HUNTER-SCHREGER BANDS IN THE ENAMEL OF *MOROPUS* (MAMMALIA: CHALICOTHERIIDAE) IN COMPARISON TO SOME OTHER PERISSODACTYLA

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Abstract

In the Chalicotheriidae the main shearing facets of upper and lower molars possess a very significant modification of the direction of Hunter-Schreger bands (HSB). In contrast to the primitive horizontal HSB orientation, chalicotheres show distinctly U-shaped HSB that intersect the main cutting edges at almost right angles. This relationship is maintained throughout the various stages of wear. This specific characteristic is shared with Brontotheriidae. Certain other Perissodactyla, such as Tapiroidea and Rhinocerotidae, but definitely not the Equoidea, follow a similar tendency. Functionally, the reorientation of the HSB is interpreted as an adaptation to reduce abrasion. The reorientation of the HSB seems to be related to interprismatic matrix (IPM) parallel to the prisms.

Zusammenfassung

Bei den Chalicotheriidae zeigen die Hauptschneidekanten der oberen und unteren Molaren eine auffallende Abweichung von der normalerweise horizontalen Orientierung der Hunter-Schreger-Bänder (HSB). Die HSB sind U-förmig gebogenen und stehen annähernd senkrecht auf den Hauptschneidekanten. Dieser Winkel bleibt durch diese spezielle Anordnung auch während der fortschreitenden Abkauung erhalten. Dieses abgeleitete Merkmal teilen die Chalicotheriidae mit den Brontotheriidae. Andere Perissodactyla, wie die Tapiroidea und Rhinocerotidae, nicht aber die Equoidea, verfolgen eine ähnliche Strategie. Funktionell wird diese Reorientierung der HSB als Anpassung gedeutet, durch die der Abrieb der Schneidekante reduziert wird. Die Reorientierung der HSB scheint an eine Interprismatische Matrix (IPM) gebunden sein, die parallel zu den Prismen liegt.

Introduction

The prismatic enamel of most large mammals is characterized by Hunter-Schreger bands (HSB). These are light and dark bands often visible in low-powered light microscopy. The SEM shows their nature as decussating layers of enamel prisms (Fig. 1). The most common orientation of these bands is roughly parallel to the alveolar surface of the jaw, which is here termed the "horizontal orientation."

In contrast to most other large mammals, several groups of perissodactyls such as Chalicotheriidae, Brontotheriidae, Tapiroidea, and Rhinocerotidae (but not Equoidea) modified the horizontal orientation of HSB. The vertical orientation of HSB in Rhinocerotidae was described by Rensberger and Koenigswald (1980) and Boyde and Fortelius (1986). Rensberger and Koenigswald (1980) interpreted the modified orientations found in Tapiroidea and Brontotheriidae as structural intermediates in the evolution toward Rhinocerotidae.

This paper describes the modified orientation of HSB in the schmelzmuster of Chalicotheriidae. The study is based on various jaws (including milk dentitions) of *Moropus elatus* and *Moropus* sp. from the Agate Springs Quarries, lower Harrison Formation, Nebraska (Holland and Peterson, 1914). The extremely well-

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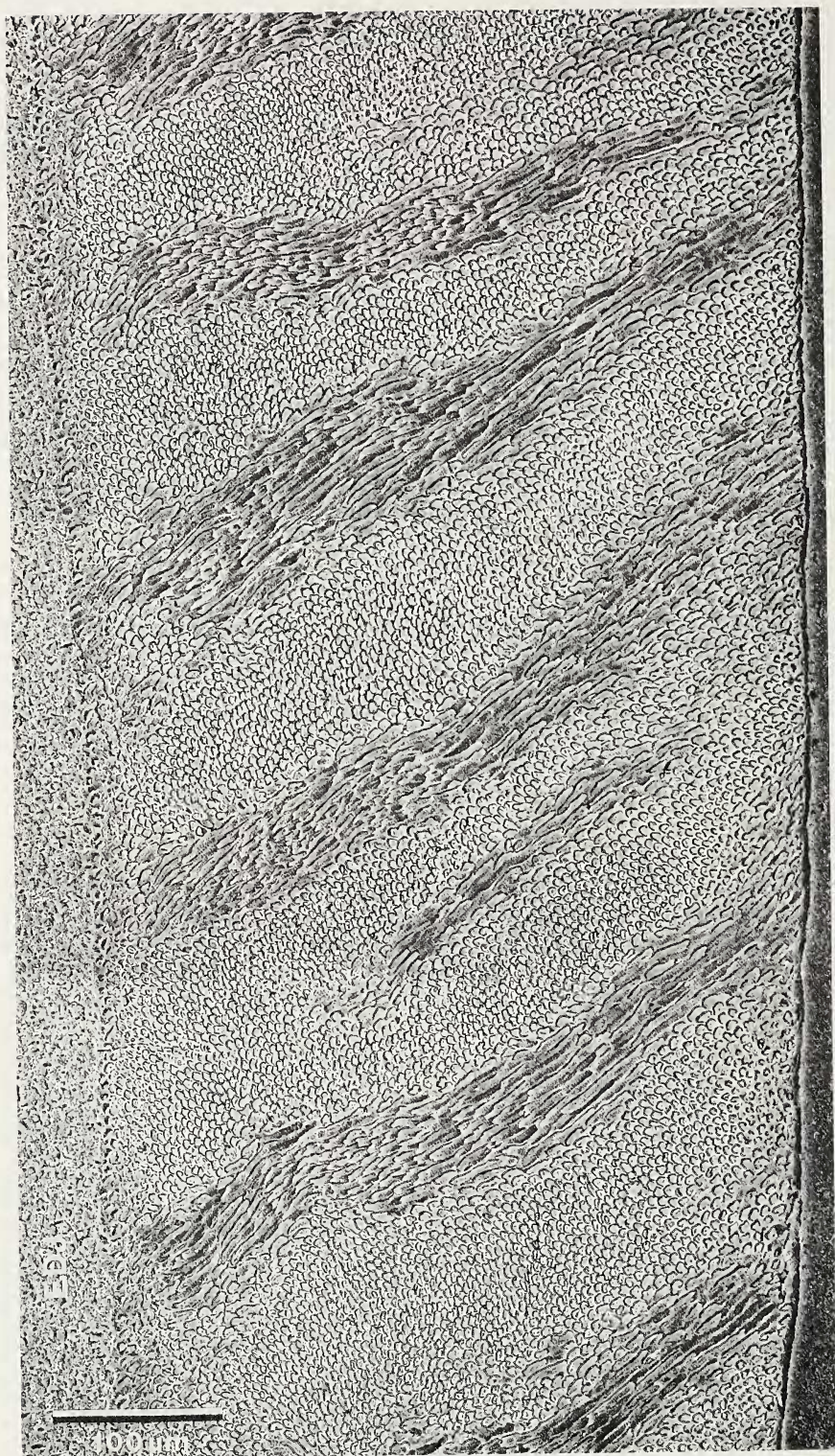
preserved enamel and the specific schmelzmuster allows a tracing of the orientation of the HSB over almost the entire surface of the teeth. The material was generously made available by the Carnegie Museum of Natural History.

The schmelzmuster of *Moropus* is compared with that of other Chalicotheriidae, Brontotheriidae, and other Perissodactyla. This survey allows a discussion of functional aspects of the orientation of HSB.

HUNTER-SCHREGER BANDS

Hunter-Schreger bands (HSB) constitute one of the basic enamel types (Koenigswald, 1980, 1982) widely distributed among mammals. This enamel type is characterized by layers of enamel prisms of regularly alternating direction. Prisms of adjacent layers often decussate at a high angle of up to 90°. The thickness of the bands counted in prism diameters is significant for rodent incisors (pauciserial, multiserial, or uniserial) (Korvenkontio, 1934; Wahlert, 1968), but shows a wide individual variation in larger mammals (Fig. 1). Average thickness between 5 and 20 prisms have been counted by Kawai (1955) for various species. Mostly commonly, thickness tends to be around ten prisms. But thickness is only one of the characters of the HSB. The bands share regular bifurcation patterns as shown in Fig. 5C, 6C, and prisms change over from one band to the next in the transitional zones between bands (Koenigswald and Pfretzschner, 1987). As seen in cross sections through the enamel, HSB often form only one layer of a given schmelzmuster and are combined with an inner and/or outer layer of radial enamel, a different enamel type in which the prisms do not decussate.

As planar elements, the HSB show two distinct directions (Fig. 2). The one observable in the vertical cross section between the enamel-dentine junction (EDJ) and the outer surface is defined as inclination (Korvenkontio, 1934). The inclination is 0° when the bands are perpendicular to the EDJ. The second direction is the lateral orientation which can be studied on the translucent enamel surface or in tangential sections through the layer with HSB. Based on commonality among Mammalia, the least derived lateral orientation is horizontal—that is, parallel to the alveolar margin of the jaws. This paper concentrates on modifications of the lateral orientation of HSB.

METHODS

Enamel prisms function like optic fibers when exposed to a strong source of light. The individual prisms are too thin to be observed under a low-powered microscope, but since all prisms within one band have the same orientation, their optic activity sums up, and HSB become visible even at low magnification. When the enamel is illuminated parallel to the bands, they become visible as light and dark areas. The prisms of all dark areas point toward the light source, whereas the prisms in light areas form a larger angle with the direction of the light (Koenigswald and Pfretzschner, 1987). By handling the tooth in front of a strong light source like fiber optics under a binocular microscope, the lateral orientation of the HSB can be studied at 20 to 50 times magnification. At the same time, the

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Fig. 1.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. Scanning electron micrograph of longitudinal section through the protoconid of the lower molar, depicting Hunter-Schreger bands of varying thickness. (EDJ = enamel dentine junction.)
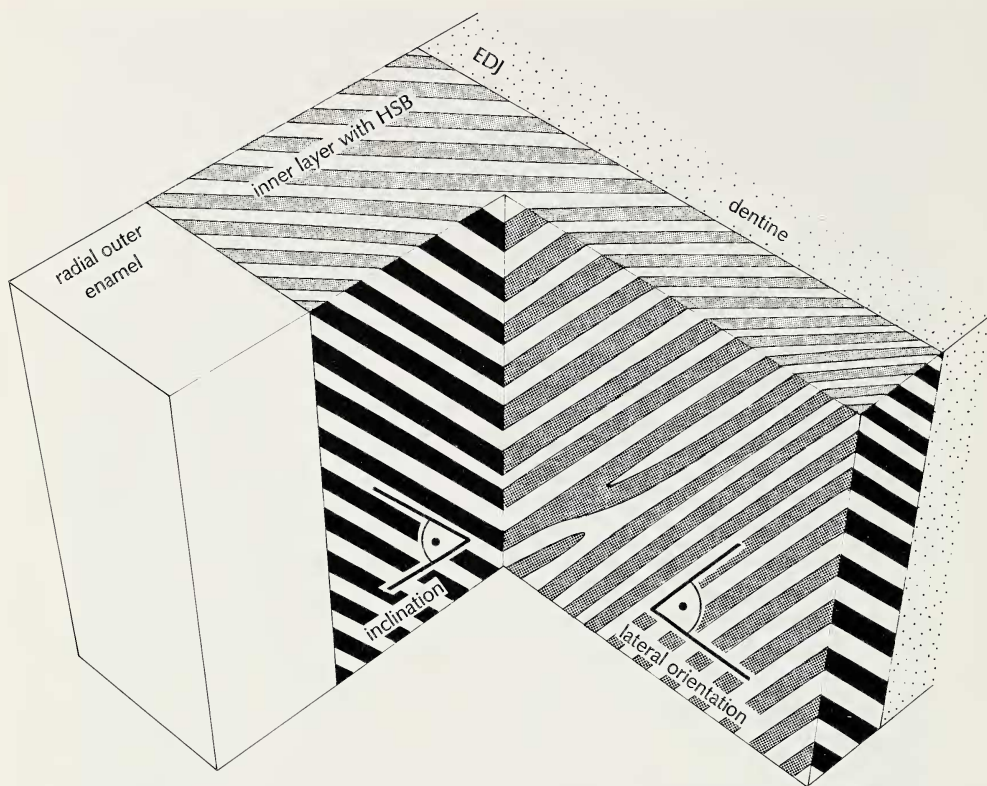
Fig. 2.—Diagram to illustrate inclination and lateral orientation of Hunter-Schreger bands (HSB). Inclination is defined as the angle between the HSB and a plane parallel to the enamel dentine junction (EDJ). It is seen best in a vertical cross section. Lateral orientation is usually horizontal but in some cases, as in chalicotheres, rotated. The HSB include an angle with the plane parallel to the alveolar margin of the jaw. In the enamel depicted here, two layers of different enamel types form the schmelz-muster, as in chalicotheres or brontotheres, having an inner layer with HSB and on outer layer with radial enamel.

unilateral bifurcation of the bands then becomes visible (Koenigswald and Pfretz-schner, 1987).

In order to facilitate the mapping of these observations, casts were made from the teeth studied and the directions of the HSB were drawn on the plaster casts as observed.

A thick layer of outer radial enamel or a structured enamel surface can often obscure the visibility of the HSB. Pericymata on the enamel surface, although occasionally parallelling the HSB, must not be mistaken for HSB, since they are fundamentally independent structures.

To study the schmelzmuster and the orientation of the HSB from sections of teeth or tooth fragments, they have to be embedded into epoxy resin, sectioned, and ground in the desired direction. On a tangential section through the layer containing HSB, the lateral orientation of the HSB can be studied even when they are not visible from the outside. The prisms show the same optical properties in sections as in surface views. These properties become even more visible when etched (e.g., with 2N HCl for 2–5 sec). The etched surfaces, coated with a con-
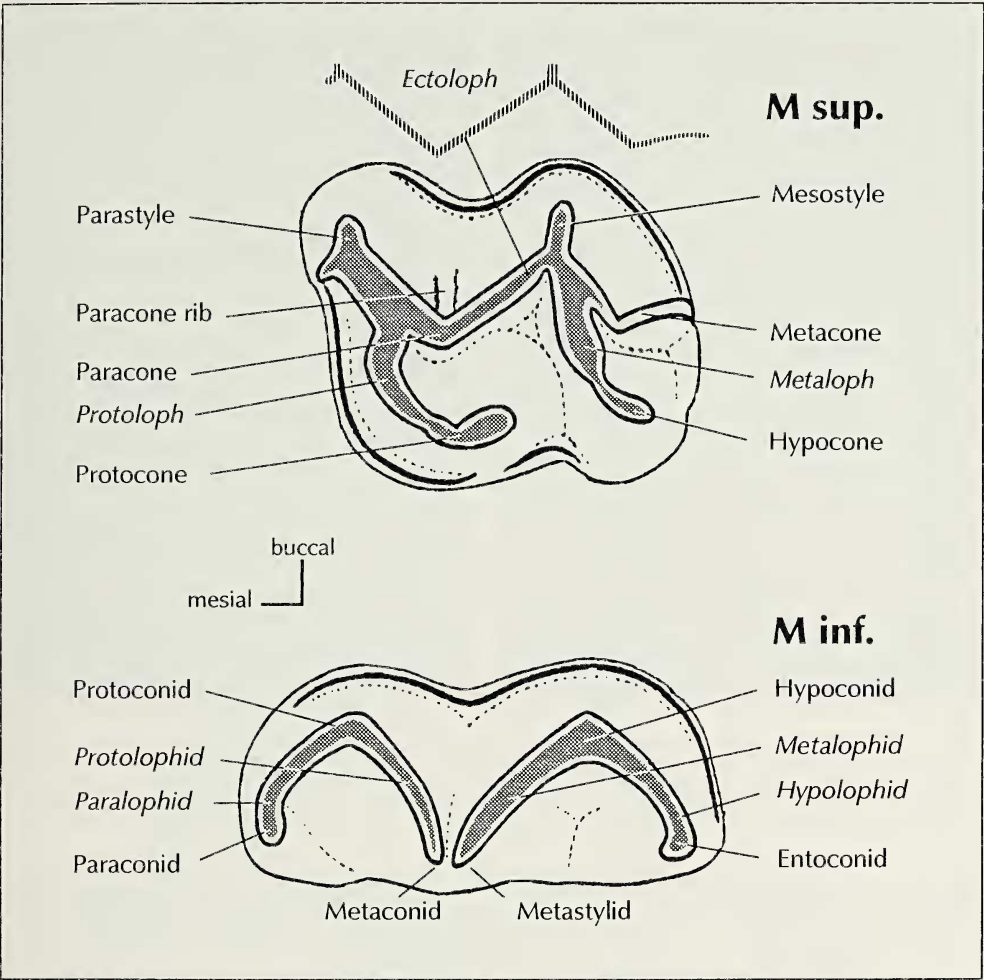
Fig. 3.—*Moropus* sp. Tooth cusps in upper and lower molars. Modified after Coombs (1978) and Thenius (1989).

ducting element (e.g., gold palladium), can be studied for further details of the complex enamel structure under the SEM.

Morphological terms used for the description of *Moropus* (Fig. 3) follow Thenius (1989) and Coombs (1978).

SCHMELZMUSTER OF *MOROPUS*

The schmelzmuster of *Moropus* is characterized by HSB that continue from the EDJ almost to the outer surface (Fig. 1). The angle of decussation is reduced in an outer zone which continues into a thin radial enamel. The inclination of the HSB is slight and concave upwards. In a tangential view of the HSB are slightly wavy and bifurcate frequently. The lateral orientation of the HSB varies: it is horizontal at the base of the crown but strongly bent to intersect the main cutting edges almost vertically. A detailed description is given below. The prisms generally
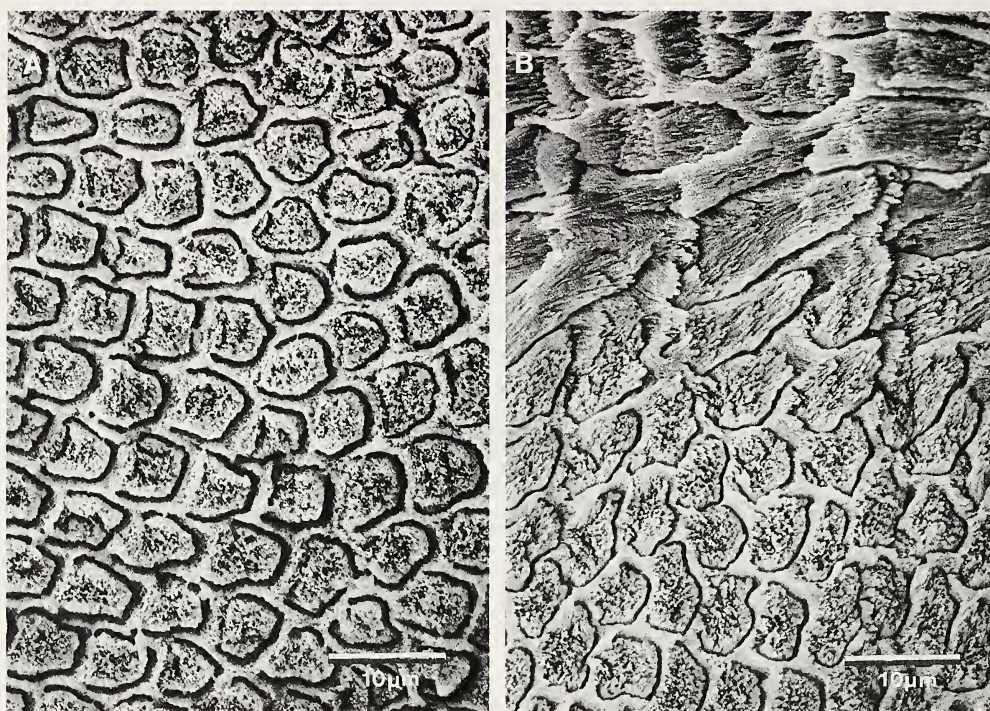
Fig. 4.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. A: SEM micrograph of enamel prism cross sections in a tangential ground and etched section of the lower molar. Most prisms have an open but somewhat irregular prism sheath. B: Prisms in cross section and longitudinal aspect at the border between HSB. The IPM is almost parallel to the prisms.

have an incomplete prism sheath (Fig. 4A). The cross section is rounded or angular. Prisms show a "seam" (Lester and Koenigswald, 1989), especially near the EDJ. The IPM crystallites run almost parallel to the prisms and surround them.

ORIENTATION OF HUNTER-SCHREGER BANDS

Upper molar morphology is characterized by a single series of shearing facets which is formed by the ectoloph (Fig. 3). While parastyle and mesostyle remain almost vertical, the paracone and metacone are strongly inclined, which results in a strong flexion of the ectoloph. The enamel on the buccal side is much thicker than on the lingual side. The protocone and the hypocone are on the lingual side. The hypocone forms a second shearing facet positioned lingually from the metacone. The protocone is only slightly linked to the ectoloph by the protoloph and forms an almost isolated rounded cusp.

In the upper molars the HSB are oriented horizontally in the cingulum and at the base of the crown. The horizontal orientation of the HSB is retained on the lingual side of the hypocone and on all sides of the protocone to its full height. On the buccal side of the ectoloph, however, the lateral orientation of the HSB is strongly modified as follows. Parastyle and mesostyle retain the horizontal HSB, but on the prominent paracone the ectoloph forms two cutting edges that enclose an angle of roughly 90°. HSB are bent in a U-shaped fashion to intersect the cutting edges at an almost right angle (Fig. 5A, C). Below the tip of the paracone
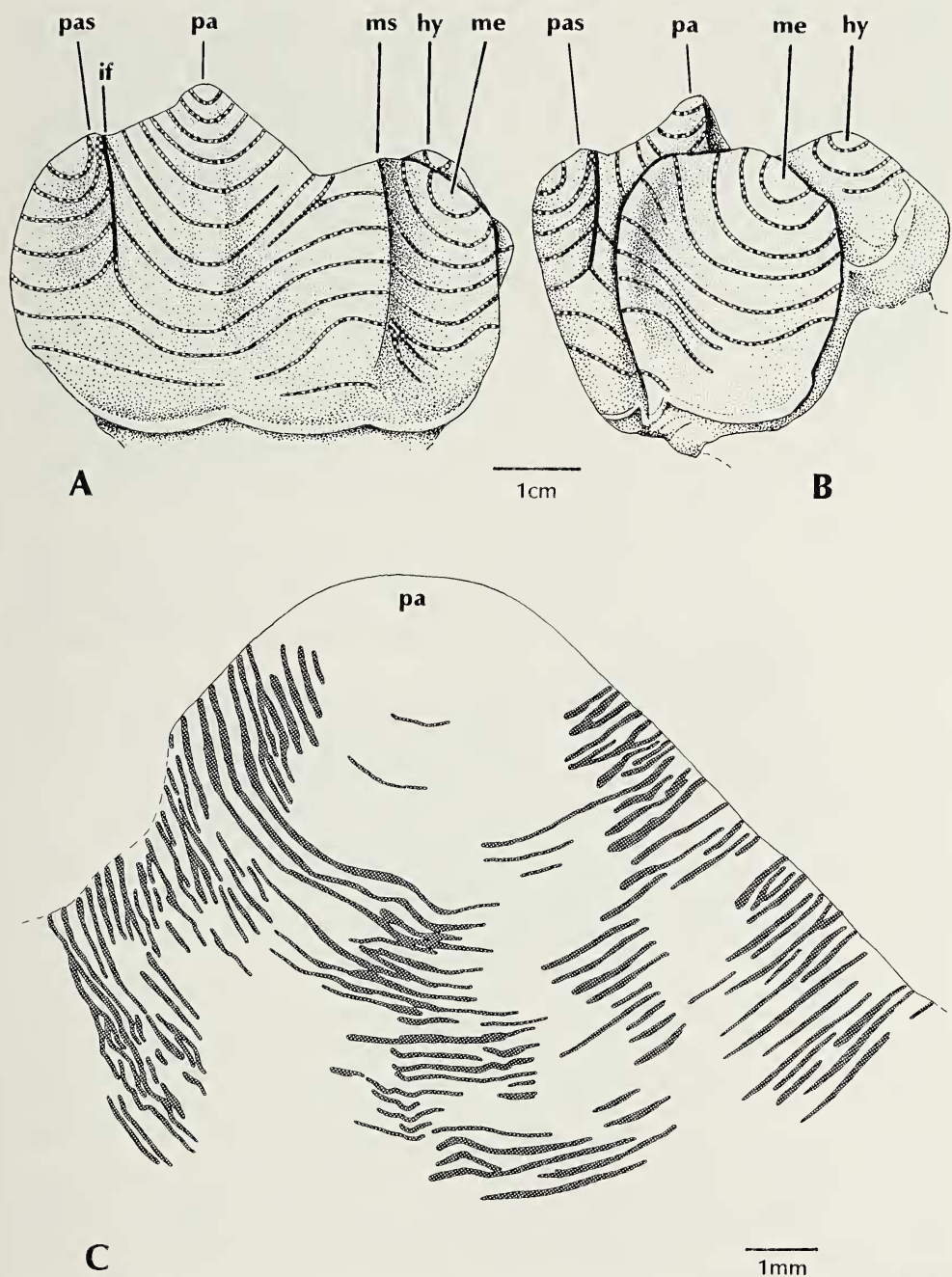
Fig. 5.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. Upper M³. A: diagrammatic HSB orientation in the ectoloph between parastyle and mesostyle. B: diagrammatic HSB orientation in the ectoloph between mesostyle and metastyle. C: detailed mapping of the U-shaped HSB orientation in the paracone (detail from A). Abbreviations: if, interface between fields of HSB; hy, hypocone; me, metacone; ms, mesostyle; pa, paracone, pas, parastyle.

the HSB pass through a short horizontal section. If the paracone rib is prominent, the HSB may even be flexed downward forming an acute angle. Between the horizontal HSB related to the paracone and the inclined HSB related to the parastyle, there is a distinct interface in which the HSB of both dental elements meet at an acute angle. This interface is marked by a slight crease in the enamel surface. But between paracone and mesostyle the fields of HSB grade into each other without a distinct border. Since HSB bifurcate frequently, such a transition from strongly inclined to horizontal HSB is made possible.

In the distal part of the ectoloph the metacone is not morphologically distinct. However, the orientation of the HSB clearly indicates the position of this cusp within the ectoloph. On the metacone the HSB orientation is similar to that of the paracone. Whereas HSB are steeply oriented on both flanks they pass through a narrow horizontal stretch below the cusp. Because of the U-shape, the HSB are again oriented almost normal to the cutting edge between metacone and mesostyle. On the other flank of the metacone they intersect the descending ectoloph at a high angle. The hypocone, which is linked to the ectoloph by the metaloph, shows a U-shaped orientation of the HSB on the buccal side. On the lingual side HSB orientation is more or less horizontal.

The upper milk dentition is generally molariform and follows the same basic pattern. In the premolars the protocone is relatively bigger and somewhat buc-colingually compressed, thus forming a short cutting edge comparable to the ectoloph. The HSB are slightly flexed and therefore approach the cutting edges at almost right angles as well.

In the lower molars trigonid and talonid form similar triangles which are connected at the twin cones of metaconid and metastylid. The W-shaped buccal side forms the shearing facets working against the ectoloph of the upper molars. The enamel is again thicker on the buccal side than on the lingual side.

The W-shaped cutting edge is formed by the paralophid, protolophid, metalo-phid, and hypolophid (Fig. 3). The base of the crown and the lingual sides of the main cusps show distinct horizontally-oriented HSB (Fig. 6A). In a protoconid and hypoconid the HSB are similarly U-shaped as in the ectoloph of the upper molars. While the HSB pass through a narrow section of the horizontal orientation and the buccal side of the protoconid and hypoconid, they bend upward toward the cutting edges on both flanks of each cone (Fig. 6A). Distinct interfaces are found between the cusps situated more to the lingual side. The interfaces are best seen in the paralophid and hypolophid separating the field of HSB related to the paraconid and protoconid and the entoconid and hypoconid, respectively (Fig. 6B, C). Distinct interfaces separate the HSB fields of the twin cusp metaconid/metastylid from that of the protoconid and hypoconid. These interfaces converge onto the central valley and do not reach the base of the crown.

The molariform P_4 and the milk teeth follow a similar pattern as far as they could be investigated. In the anterior premolars (P_2 and P_3) the HSB are slightly flexed towards the shearing facets. In the incisors of the lower jaw HSB are all horizontally oriented.

The pattern described above was found in all available teeth of *Moropus elatus* and *Moropus* sp. as well as in the European *Chalicotherium goldfussi* and the Asian *Chalicotherium* cf. *habereri*. The congruence of this character in several related genera excludes the possibility that the U-shaped HSB orientation is an individual variation and implies that it is characteristic of the Chalicotheriidae in general. Individual variation within the group occurs on a much smaller scale, and concerns the thickness, bifurcation, and exact orientation of HSB.
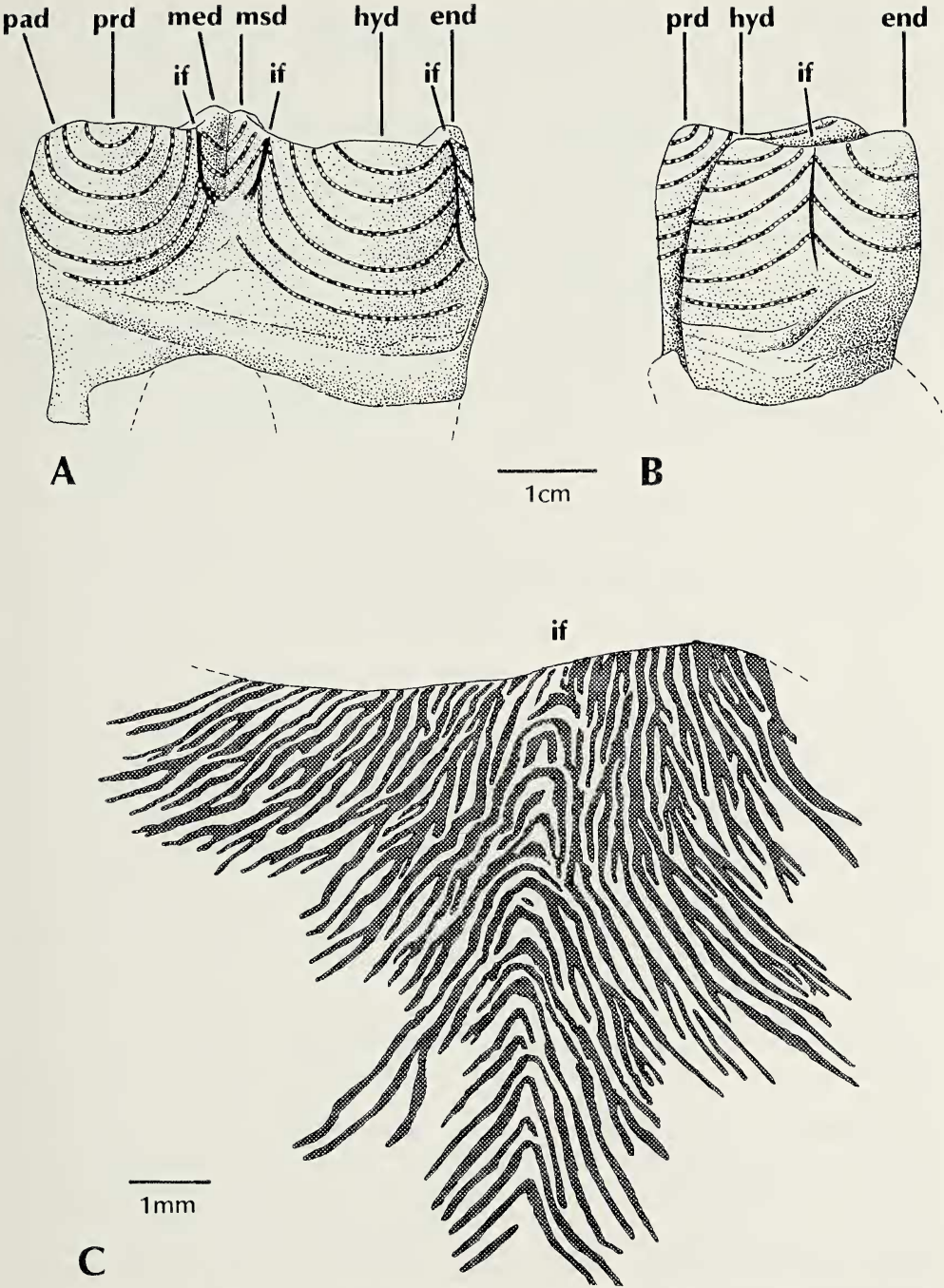
Fig. 6.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. Lower M_1. A: diagrammatic HSB orientation on the buccal side. B: schematic HSB orientation on the hypolophid with interface. C: detailed mapping of the HSB orientation in the hypolophid with an interface between areas of the hypoconid and entoconid. Abbreviations: end, entoconid; if, interface between fields of HSB; hyd, hypoconid; med, metaconid; msd, metastylid; pad, paraconid; prd, protoconid.

ORIENTATION OF THE HSB IN
OTHER PERISSODACTYLS

Equoidea

In the well-documented evolution of the Equidae, the HSB consistently retain a horizontal orientation. The basic schmelzmuster, as in *Hyracotherium,* shows horizontal HSB penetrating from the EDJ almost to the outer surface where a thin radial enamel is found. The crystallites of the IPM run parallel to the prisms (Pfretzschner, 1993, in press). In *Mesohippus* and *Anchitherium* this basic schmelzmuster is retained, but the IPM crystallites form an angle with prisms and are arranged in inter-row sheets.

When the molars of Equidae become hypsodont as in *Merychippus, Hipparion,* or *Equus,* the schmelzmuster is reorganized. A layer of "modified radial enamel" characterized by thick, vertical inter-row sheets is introduced between the EDJ and the layer of HSB (Pfretzschner, 1993, in press; Koenigswald et al., 1993). Nevertheless, the horizontal orientation of the HSB is retained unchanged.

Palaeotherium sp. (Palaeotheriidae) shows well-developed HSB (Remy, 1976) which are generally oriented horizontally. Although the paracone and metacone in the ectoloph of the upper molars are similarly inclined and shaped as in *Moropus,* the HSB retain their horizontal orientation (Fig. 7A). This documents that HSB orientation is independent of the shape of the ectoloph.

Brontotheriidae

In comparison to the Chalicotheriidae studied, the enamel in the larger Brontotheriidae, such as *Menodus proutii,* is fairly thick. The schmelzmuster of Brontotheriidae is in most cases two-layered. An inner layer is formed by HSB which are only very slightly inclined toward the occlusal surface concave up. The thickness of HSB with an oblique lateral orientation is difficult to quantify since the likelihood of finding these bands at an angle other than 90° is very high. The thickness counts therefore are commonly too high. The HSB disappear in the outer layer of radial enamel. This outer layer is almost as thick as the inner layer and prevents observation of the HSB from the outer surface of the enamel.

The prisms of the radial enamel rise apically at a maximum of about 45°. The prisms have incomplete prism sheaths and the IPM is mainly parallel to the prisms.

In areas with thin enamel, the outer radial enamel may be reduced in thickness or missing. On the occlusal surface, however, the outer radial enamel on the outside is worn off more rapidly than the inner layer of HSB. Therefore, the direction of the HSB can be observed near the occlusal surface. In the angled ectoloph of the upper molars, a U-shaped orientation is found at the paracone and the metacone as described for *Moropus.* In lower molars a similar U-shaped orientation of the HSB is found at the hypoconid and the protoconid just as in *Moropus.* In the paralophid, protolophid, metalophid, and hypolophid, interfaces with very sharp turns of the HSB are present as described for the Chalicotheriidae. These interfaces are visible at the occlusal surface but can be observed better in a tangential ground section.

Tapiroidea

The schmelzmuster of *Tapirus* (Tapiridae) is characterized by horizontal HSB which extend to the outer surface. The prisms show an open prism sheath and
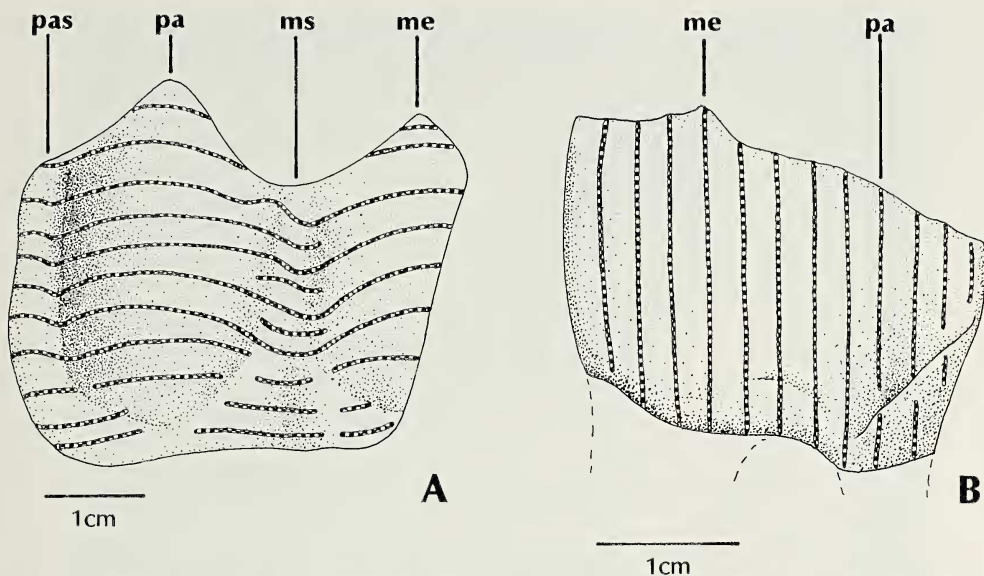
Fig. 7.—Hunter-Schreger band orientation in Equoidea and Rhinocerotidae. A: *Palaeotherium* sp. (Equoidea) Frohnstetten, Germany, lower Oligocene. Diagrammatic illustration of the horizontal HSB orientation in the ectoloph of an upper molar. B: *Floridaceras whitei* (Rhinocerotidae). Diagrammatic illustration of the vertical HSB in the ectoloph of an upper molar. Abbreviations: me, metacone; ms, mesostyle; pa, paracone; pas, parastyle.

are surrounded by IPM, the crystallites of which are almost parallel to the prisms. HSB orientation is modified in *Tapirus* which was discussed for lower molars by Rensberger and Koenigswald (1980). In the lower molars, the HSB of the lingual and buccal sides of the main cusps are horizontal. In the transverse lophs, the HSB bend into an almost vertical direction. In the middle lophs, the fields of HSB of the two involved cusps meet at a distinct interface which often can be seen in the worn occlusal surface as the angle between HSB (Fortelius, 1984: fig. 2b) or on the unworn surface as a slight groove (Fig. 8).

In the upper molars, the horizontal HSB dominate. Only in the uppermost parts of the transverse lophs can similar orientations of the HSB and incipient interfaces be observed.

In *Colodon cingulatus* (Helatelidae) from the Oligocene of Montana, a similar schmelzmuster was found (Rensberger and Koenigswald, 1980), but no material for sectioning was available.

Lophiodon lautricense (Lophiodontidae), a large tapiroid from the Eocene of Europe, follows the tapiroid schmelzmuster, even though an outer zone of radial enamel occurs in some parts of the molars. The prism sheath is generally incomplete and the IPM is parallel to the prisms.

In the upper molars the horizontal HSB are widely retained. Only in the transverse lophs do the HSB turn into a vertical position. Interfaces were not seen in the available material. In the lower molars the protoconid and the hypoconid show horizontal HSB. Toward the transverse lophs, the HSB turn vertically. Interfaces are well-marked by a slight groove in the enamel surface and on the occlusal surface by an irregularity of the HSB. The lower molars have horizontal HSB which are strongly modified in the lingual walls of metaconid and entoconid.

Fig. 8.—*Tapirus priscus*, Eppelsheim, Germany, Upper Miocene. Unretouched photo of the anterior loph of the lower right M_3 with horizontal HSB in the cusps, inclined HSB in the loph and an interface in the center of the loph where the areas of protoconid (left) and metaconid (right) merge into each other. Length of bar equals 5 mm.

Heavy undulation of the HSB forms vertical structures in the outer enamel. These unusual structures resemble the modification of HSB found in hyaenids (personal observation).

Rhinocerotidae

The schmelzmuster in the molars of most rhinos (e.g., *Coelodonta antiquitatis*) consists of an inner layer of HSB and an outer layer of radial enamel. The outer layer varies considerably in different genera. It can be very thin or even missing as in *Subhyracodon* or *Floridaceras whitei*.

Rhinocerotid upper and lower molars are characterized by vertical HSB as in *Floridaceras whitei* (Fig. 7B). The vertical orientation is not restricted to certain parts of the occlusal surface as in Chalicotheriidae, Brontotheriidae, or Tapiroidea, but continues around the entire tooth and does not include any interfaces. These HSB bifurcate in the same manner as horizontal HSB. These vertical HSB have been studied by Rensberger and Koenigswald (1980) and Boyde and Fortelius (1986). The authors were not aware that this peculiar structure in rhino teeth, which results in a specific roughness of the occlusal surface, was already observed and carefully figured more than 100 years earlier by Quenstedt (1867: pl. 1:1, pl. 2:35).

In incisors the HSB are horizontal but intersect the very steep shearing facets at nearly right angles (Koenigswald, 1985; Koenigswald and Clemens, 1992). In *Coelodonta*, the prisms have incomplete prism sheaths and the IPM is mostly parallel to the prisms.

Based on the enamel surface investigation of a mandible of *Metamynodon* sp.

Table 1.—*Perissodactyl tooth material investigated in this study. 1, investigated by light microscopy on natural surfaces only; 2, investigated in sections under light microscope and SEM.*

Chalicotheriidae

Moropus elatus, Agate Springs quarries, Nebraska; Harrison Formation, Miocene; Carnegie Museum of Natural History; 1.

Moropus sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene; Carnegie Museum of Natural History; 1+2 [KOE 1436].

Chalicotherium goldfussi, Eppelsheim, Germany; Upper Miocene; Hessisches Landesmuseum, Darmstadt; 1.

Chalicotherium cf. *haberreri,* Pavlowelar, Kazahkstan; Turolian; Paleontological Museum, Moscow; 1.

Equoidea

Hyracotherium sp., Bighorn Basin, Wyoming; Willwood Formation, lower Eocene; U.S. Geological Survey, Denver; 1+2 [KOE 1022].

Equus sp., Heidenheim, Germany; upper Pleistocene; 1+2 [KOE 34].

Palaeotherium sp., Frohnstetten, Germany; Oligocene; 1+2 [KOE 1666].

Brontotheriidae

Menodus proutii, White River, Nebraska; Oligocene; Hessisches Landesmuseum, Darmstadt; 1.

large brontothere, gen. indet., Nebraska; Chadron Formation, White River Group, Nebraska; Nebraska State Museum, Lincoln; 1+2 [KOE 1637].

Tapiroidea

Tapirus priscus, Gau Weinheim, Germany; upper Miocene; Hessisches Landesmuseum, Darmstadt; 1.

Tapirus priscus, Esselborn, Germany; upper Miocene; Hessisches Landesmuseum, Darmstadt; 1.

Tapirus sp., China; Pleistocene; 1+2 [KOE 73].

Colodon cingulatus, Oligocene, Montana; Carnegie Museum of Natural History; 1.

Lophiodon lautricense, Robiac, France; late Eocene; Hessisches Landesmuseum, Darmstadt; 1.

Rhinocerotidae

Ceratotherium simum, Africa; Recent; 1+2 [KOE 610].

Rhinoceros sp., Sangiran Java; Pleistocene; 1+2 [KOE 71].

Coelodonta antiquitatis, Urspringhöhle, Germany; 1+2 [KOE 52].

Subhyracodon occidentale, M^3; Museum of Comparative Zoology, Harvard University; 1+2 [KOE 356].

Floridaceras whitei, Hawthorne Formation; Miocene; Thomas Farm, Florida; Museum of Comparative Zoology, Harvard University; 1+2 [KOE 357].

(Amynodontinae), the HSB orientation and the schmelzmuster seem to follow the same pattern as Rhinocerotidae.

DISCUSSION

Hunter-Schreger bands were evolved several times in parallel among various mammalian lineages (Koenigswald and Clemens, 1992), for instance in the early Paleocene by condylarthrans (Koenigswald et al., 1987), in primates, carnivores, rodents, and a few marsupials. Despite this multiple origin, the usual orientation of HSB is horizontal. Therefore this orientation is regarded as the most primitive condition for mammals in general as well as for perissodactyls.

The interpretation of the variability of the schmelzmuster among the Perissodactyla from a phylogenetic perspective allows us to differentiate the derived genera within the various families and superfamilies, respectively. The Equoidea retain the horizontal HSB. However, when the molars become hypsodont, a significant layer of modified radial enamel is introduced between the EDJ and

the layer of HSB. This schmelzmuster developed convergently in several other large herbivores with hypsodont molars (Pfretzschner, in press; Koenigswald et al., 1993). These large herbivores share the characteristic of having the IPM at a high (close to 90°) angle with the prisms.

Other Perissodactyla, such as Brontotheriidae, Chalicotheriidae, Tapiroidea, and Rhinocerotidae, follow different pathways of modification in their schmelzmuster. Brontotheriidae, widely accepted to be closely related to Equoida, keep the crystallites of the IPM parallel to the prisms and develop the U-shaped orientation of the HSB. The strongly curved HSB intersect the occlusal surface at almost right angles. They share this derived character with the Chalicotheriidae. Differences between some Chalicotheriidae and Brontotheriidae are expressed mainly in the thickness of the outer radial enamel. Whether the very similar orientation of the HSB in both families is a synapomorphy must be tested by a larger survey of the schmelzmuster in both groups.

In Tapiroidea the HSB turn in a vertical direction only in the transverse lophs immediately below the crest. *Tapirus* and *Lophiodon* differ in the enamel on the lingual side of the lower molars.

The Rhinocerotidae have a very derived schmelzmuster with vertical HSB. The vertical orientation of HSB in Rhinocerotidae is unique among Perissodactyla. However, a similar orientation evolved convergently in astrapotheres (Fortelius, 1984, 1985; Rensberger and Pfretzschner, 1992), but not in *Arsinoitherium* as assumed by Fortelius (1984) and since disproven by Pfretzschner (in press).

Whereas in the Rhinocerotidae the HSB are vertical around the entire molars, in tapirs, chalicotheres, and brontotheres, the HSB of the various cusps developed vertical HSB individually. The interfaces, found as distinct lines between the cusps even when they are united in the same loph, are the most obvious feature indicating this different strategy.

Hyracoidea, which are regarded by some as a sister group of the Perissodactyla (Fischer, 1986), have a horizontal HSB orientation in some genera (Fortelius, 1985), but, astonishingly, most genera lack HSB altogether.

A strong functional significance of the modified orientation of the HSB in perissodactyls is indicated first by the restriction of the modifications to the main cutting edges, and second by the parallel occurrence of this tendency in several lineages such as in Chalicotheriidae, Brontotheriidae, Tapiroidea, and Rhinocerotidae. The functional significance here is that the HSB intersect the main shearing facets at almost right angles. The modified orientation of HSB brings a large number of prisms into a direction favorable for reduced wear (Rensberger and Koenigswald, 1980; Boyde and Fortelius, 1986). This modification has reached its greatest perfection in the Rhinocerotidae, but is not found in Equoidea or any member of the Artiodactyla.

Even if the teeth are to some extent worn, the high angle between the cutting edge and the HSB is maintained in chalicotheres and brontotheres and especially in Rhinos.

Three apparently antagonistic hypotheses were formulated to explain the adaptive significance of vertical HSB in Rhinocerotidae. Rensberger and Koenigswald (1980) argued that the vertical HSB allow a maximum number of prisms to intersect the occlusal surface at almost right angles. Their experimental data demonstrated that there is less abrasion of the enamel when prisms are at right angles to the occlusal surface compared to prisms parallel to the occlusal surface. Pfretzschner (1992, in press) argues that vertical HSB would ideally compensate mas-

ticatory stresses in the enamel of hypsodont teeth near the EDJ. Rensberger (1992), on the other hand, argues that the maximum tensile stresses in the flat lophs of rhinos are normal to the cutting edges, causing fracturing parallel to the edges. Orientation of the HSB perpendicular to these edges resists such fracturing. The material studied here makes it possible for us to evaluate these hypotheses.

Vertical HSB were achieved in Rhinocerotidae and Astrapotheriidae in low-crowned molars. Since this character antedates hypsodonty in both lineages, it cannot be an adaptation specifically related to hypsodonty. Vertical HSB, which are found to reduce abrasion in the cutting edges, are not unique to Perissodactyla. A similar orientation of HSB as in Tapiroidea has been found in the carnassials of some Carnivora, in which the horizontal HSB change direction abruptly when they approach the cutting edge to intersect the blades of the carnassial notch vertically.

There is a general demand to stabilize the cutting edges, especially in low-crowned teeth, to keep the functional apparatus in shape. Wear of the oblique cutting edges in low-crowned teeth, in Chalicotheriidae and in Brontotheriidae but also in Carnivora, changes the morphology of teeth significantly and demands a readjustment of the antagonist. The specific quality of high-crowned teeth is that, due to the almost vertical cutting edges, the morphology of the occlusal surface is maintained during progressive wear for a relatively long time. If wear of cutting edges is reduced by prisms penetrating at high angles (as in vertical HSB), a strong selective pressure applies to HSB reorientation from horizontal to U-shaped or vertical.

However, this explanation does not contradict the hypothesis of Pfretzschner (in press). The animals with vertical HSB in the entire molars, such as the early, low-crowned Rhinocerotidae, have an appropriate prerequisite to build hypsodont molars. This prerequisite is present in the Rhinocerotidae and the Astrapotheriidae. According to Pfretzschner's hypothesis, most other herbivores, like horses or bovids, that evolved hypsodont molars but retained horizontal HSB introduced the "modified radial enamel" close to the EDJ. In the modified radial enamel, thick layers of IPM lie between rows of prisms. These layers therefore were called "inter row sheets" by Boyde (1964). It is mechanically important that the crystallites of the IPM are at a high angle to the prisms. The thick descending layers of IPM in the modified radial enamel and the rows of ascending prisms function very similarly to vertical HSB. The orientation of structural elements is very important since the enamel is very anisotropic in its physical properties.

Among small mammals, some rodent lineages modify the enamel of their incisors from primarily horizontal uniserial HSB to vertical HSB. Several different pathways to achieve this character can be distinguished in the Myoxidae, Dipdidae, and Spalacidae (Koenigswald, 1993). The functional significance of these modifications in the very thin rodent enamel is not yet fully understood. The uniserial HSB with an IPM at right angles to the bands seems to be functionally more isotropic to crack propagation than the thick HSB of the larger mammals.

Modification of the primarily horizontal HSB occurs only occasionally among large mammals. The occurrence in Perissodactyla is unusually frequent. Obviously, with exception of Equoidea, most other groups in the Perissodactyla change HSB orientation instead of introducing a large angle between the IPM and the prisms. They share this character with astrapotheres. Therefore, the modification of HSB orientation seems to be linked to IPM parallel to the prisms. In contrast to the modified radial enamel, which is linked to the ability to reorient the crys-

tallites of the IPM at an angle to the prisms, the lateral reorientation of the HSB demonstrates second pathway to strengthen the enamel in cases when IPM crystallite orientation cannot be changed.

This study of HSB orientation in Perissodactyla demonstrates that the quality of enamel is a source of functional as well as phylogenetic information. Neither aspect excludes the other since the evolution of characteristics always has to have some functional significance if the new combination of characteristics is to be advantageous for the animal. It is especially true in enamel that many characteristics evolved in parallel in various lineages that indicate such functional aspects. On the other hand, different groups often solve similar functional problems in different pathways. This allows us to identify taxonomic groups of higher rank, e.g., at the genus or family level.

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LITERATURE CITED

BOYDE, A. 1964. The structure and development of mammalian enamel. Unpublished Ph.D. thesis, University of London, London.

BOYDE, A., AND M. FORTELIUS. 1986. Development and function of rhinoceros enamel. Zoological Journal of the Linnean Society, 87:181–214.

COOMBS, M. C. 1978. Reevaluation of early Miocene North American *Moropus* (Perissodactyla, Chalicotheriidae, Schizotheriinae). Bulletin of Carnegie Museum of Natural History, 4:1–62.

FISCHER, M. S. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. Zugleich ein Beitrag zur Anpassungsgeschichte der Procaviidae. Courier Forschungsinstitut Senckenberg, 84:1–132.

FORTELIUS, M. 1984. Vertical decussation of enamel prisms in lophodont ungulates. Pp. 427–431, *in* Tooth Enamel IV (R. W. Fearnhead and S. Suga, eds.), Elsevier Science Publishers, Amsterdam.

———. 1985. Ungulate cheek teeth: Developmental, functional and evolutionary interrelations. Acta Zoologica Fennica, 180:1–76.

HOLLAND, W. J., AND O. A. PETERSON. 1914. The osteology of the Chalicotheroidea with special reference to a mounted skeleton of *Moropus elatus* Marsh, now installed in the Carnegie Museum. Memoirs of the Carnegie Museum, 3:189–406.

KAWAI, N. 1955. Comparative anatomy of bands of Schreger. Okajimas Folia anatomica Japanonica, 27:115–131.

KOENIGSWALD, W. v. 1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 539:1–129.

———. 1982. Enamel structure in molars of Arvicolidae (Rodentia) a key to functional morphology and phylogeny. Pp. 109–122, *in* Teeth: Form, Function and Evolution (B. Kurtén, ed.), Columbia University Press, New York.

———. 1985. Evolutionary trends in the enamel of rodent incisors. Pp. 403–422, *in* Teeth: Form, Function and Evolution (B. Kurtén, ed.), Columbia University Press, New York.

———. 1993. Die Schmelzmuster in den Schneidezähnen er Gliroidea (Gliridae und Seleviniidae, Rodentia, Mammalia) und ihre systematische Bedeutung. Zeitschrift für Säugetierkunde, 58:92–115.

KOENIGSWALD, W. v., AND W. A. CLEMENS. 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. Scanning Microscopy, 6(1):195–218.

KOENIGSWALD, W. v., AND H. U. PFRETZSCHNER. 1987. Hunter-Schreger-Bänder im Zahnschmelz von Säugetieren: Anordnung und Prismenverlauf. Zoomorphology, 106:329–338.

KOENIGSWALD, W. V., J. M. RENSBERGER, AND H. U. PFRETZSCHNER. 1987. Changes in the tooth enamel of early Paleocene mammals allowing increasing diet diversity. Nature, 328:150–152.

KOENIGSWALD, W. V., T. MARTIN, AND H. U. PFRETZSCHNER. 1993. Phylogenetic interpretations of enamel structures in mammalian teeth—possibilities and problems. Pp. 303–314, *in* Mammal Phylogeny; Placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.), Springer-Verlag, New York.

KORVENKONTIO, V. A. 1934. Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne. Annales Zoologici Societati Zoolgicae-Botanicae Fennicae Vanamo, 2:1–274.

LESTER, K. S., AND W. V. KOENIGSWALD. 1989. Crystallite orientation discontinuities and the evolution of mammalian enamel—Or, when is a prism? Scanning Microscopy, 3(2):645–663.

PFRETZSCHNER, H. U. 1992. Enamel microstructure and hypsodonty in large mammals. Pp. 147–162, *in* Structure, Function and Evolution of Teeth (P. Smith and E. Tchernov, eds.), Freund Publishing House, London, Tel Aviv.

————. 1993. Enamel microstructure in the phylogeny of Equidae. Journal of Vertebrate Paleontology, 13:342–349.

————. In press. Biomechanik der Schmelzmikrostruktur in den Backenzähnen von Großsäugern. Palaeontographica.

QUENSTEDT, F. A. 1867. Handbuch der Petrefaktenkunde. Laupp'sche Buchhandlung, Tübingen.

REMY, J. A. 1976. Étude comparative des structures dentaires chez les Palaeotheridae et divers autres perissodactyles fossiles. Theèse de l'Université Louis Pastuer, Strasbourg I.

RENSBERGER, J. M. 1992. Relationship of chewing stress and enamel microstructure in rhinocerotoid cheek teeth. Pp. 163–183, *in* Structure, Function and Evolution of Teeth (P. Smith and E. Tchernov, eds.), Freund Publishing House, London, Tel Aviv.

RENSBERGER, J. M., AND W. V. KOENIGSWALD. 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology, 6(4):477–495.

RENSBERGER, J. M., AND H. U. PFRETZSCHNER. 1992. Enamel structure in astrapotheres and its functional implications. Scanning Microscopy, 6(2):495–510.

THENIUS, E. 1989. Zähne und Gebiß der Säugetiere. Handbuch der Zoologie (De Gruyter, Berlin, New York), 8(56):1–513.

WAHLERT, J. H. 1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and Recent rodent groups. Breviora, 309:1–18.